

ECOLOGICAL ROLES

In a given ecoregion, ecological roles of biological soil crusts can vary widely in their importance and will depend on crust composition and biomass, as well as characteristics of the specific ecosystem being considered.

3.1 Species Composition and Biomass

The relative importance of biological crusts and their different ecological roles within an ecosystem is highly dependent on relative cover of various crustal components. For example, carbon inputs are higher when mosses and lichens are present than when the crust is dominated by cyanobacteria. Nitrogen inputs are higher with greater cyanobacterial biomass and greater cyanolichen cover. Water infiltration and soil surface stability are related to cyanobacterial biomass as well as moss and lichen cover.

3.2 Carbon Fixation

Biological soil crusts can be an important source of fixed carbon on sparsely vegetated areas common throughout western North America (Beymer and Klopatek 1991). While vascular plants contribute organic matter to soils directly beneath them, large interspaces between plants receive little plant material input. Where biological soil crusts are present, carbon contributed by these organisms helps keep plant interspaces fertile, providing energy sources for soil microbial populations.

Crustal organisms are physiologically active only when wet, and metabolic functions begin almost immediately. Respiration begins less than 3 minutes after wetting, while photosynthesis reaches full activity after 30 minutes or more. Soil oxygen concentrations, a by-product of photosynthesis, reach steady states within 1 to 2 hours of wetting (Garcia-Pichel and Belnap 1996). Rain during hot months can place lichens in a state of carbon deficiency, as the lichens can dry out before photosynthesis has begun. Jeffries et al. (1993a, b) showed cyanobacterial crusts from the Colorado Plateau had positive carbon balances only during prolonged wet periods, such as winter and spring, and that short-term wet-dry cycles, which often occur in low-elevation inland sites during summer, resulted in net carbon loss for both *Microcoleus*- and *Scytonema*-dominated crusts (this would also be expected for *Collema* and other soil lichens). Consequently, timing

and duration of precipitation may heavily influence carbon budgets in crustal organisms and thus influence the distribution of individual species.

Winter-rain deserts (e.g., Mojave and Great Basin) have a rich soil lichen flora, with the cyanobacterial flora heavily dominated by *Microcoleus*. In contrast, summer-rain deserts (e.g., Sonoran) have only a small subset of the lichens found in winter-rain deserts, while the cyanobacterial flora is a complex community co-dominated by up to 10 species. Different responses to timing and amount of precipitation and temperature may mean species composition will shift in response to predicted climate changes. Since many areas that are currently winter-rain dominated are predicted to receive increased summer rain, effects of climate change may be reflected in different soil crust composition than that currently found in the summer-rain versus the winter-rain deserts.

Soil lichens have several different strategies to optimize carbon gain (Lange et al. 1992, 1994, 1997). While photosynthesis is activated at low-water content for all species, each varies in response to higher water content. Cyanolichens, such as *Collema tenax*, showed dramatic drops in carbon fixation when water content exceeded 60 to 80%. Conversely, green algae generally showed little, if any, depression at high-water content. Water-holding capacity varies between lichens and will also influence time of carbon fixation for a given species.

Table 3.1 Common nitrogen-fixing lichens and cyanobacteria in cool and hot deserts of the western U.S.

Cool Deserts	Hot Deserts
Lichens	
<i>Collema coccophorum</i>	<i>Collema coccophorum</i>
<i>Collema tenax</i>	<i>Collema tenax</i>
<i>Heppia</i>	<i>Heppia</i>
<i>Leptochidium albocilitatum</i>	<i>Peltula</i>
<i>Leptogium</i>	
<i>Massalongia carnosa</i>	
<i>Pannaria</i>	
<i>Peltigera</i>	
<i>Polychidium</i>	
Cyanobacteria	
<i>Microcoleus vaginatus</i> (non-heterocystic)	<i>Schizothrix</i> (heterocystic)
<i>Nostoc</i> (heterocystic)	<i>Nostoc</i> (heterocystic)
<i>Scytonema</i> (heterocystic)	<i>Scytonema</i> (heterocystic)

Photosynthetic rates are also dependent on temperature (Rychert et al. 1978; Lange 1980; Nash et al. 1982; Nash and Moser 1982; Lange et al. 1997). Photosynthetic rates increase with increasing temperatures to about 28°C, above which rates decline dramatically. *Collema tenax* is an exception, with no such decline seen up to 36°C.

3.3 Nitrogen Fixation

Nitrogen concentrations are known to be low in desert soils compared to other ecosystems. Total atmospheric input over the past 10,000 years has been conservatively estimated at about 3 kg nitrogen/m², with 77% lost through wind erosion, ammonia volatilization, nitrification, and denitrification (Peterjohn and Schlesinger 1990). Extensive surveys in cool deserts have revealed only a few nitrogen-fixing plants (Farnsworth et al. 1976; Wullstein 1989). Since nitrogen can limit net primary productivity in many desert ecosystems (Ettershank et al. 1978; James and Jurinak 1978; Romney et al. 1978; Nobel et al. 1988), maintaining normal nitrogen cycles is critical to soil fertility and prevention of desertification (Dregne 1983).

Cyanobacteria and cyanolichens can be an important source of fixed nitrogen for plants and soils in desert ecosystems (Evans and Ehleringer 1993; Belnap 1995). Many biological soil crusts in western North America are dominated by nitrogen-fixing cyanobacteria and lichens (Table 3.1). These organisms are capable of both light and dark nitrogen fixation (Rychert and Skujins 1974; Pearson et al. 1981; Paerl 1990; Belnap 1994). Nitrogen fixation is highly dependent on past and present water and light regimes, as well as species composition (Rychert et al. 1978; Belnap 1994). Fixation rates are highest after photosynthesis has replenished lichen carbon stores. For most lichen species, nitrogen-fixation rates increase with temperature to 25°C, given sufficient moisture. Since nitrogen-fixation rates depend on the cover of specific crust species, timing, extent, and type of past disturbance are also critical factors (Belnap 1995, 1996). Nitrogen-fixation rates in biological soil crusts have been estimated at 2 to 365 kg/ha annually (Mayland et al. 1966; MacGregor and Johnson 1971; Rychert and Skujins 1974; Eskew and Ting 1978; Jeffries et al. 1992), with recent studies indicating that higher rates are probably more accurate (Belnap, unpublished data). Still, rates are expected to vary greatly, depending on the species present and environmental conditions.

Five to 88% of nitrogen fixed by *Nostoc* has been shown to leak into the surrounding substrate (Magee and Burris 1954; Silvester et al. 1996; Belnap et al. 1997). Nitrogen released from crustal



Figure 3.1 *Disturbance plots on the Colorado Plateau showing the difference in soil surface color between undisturbed (dark) and disturbed (light) plots. Note that the undisturbed plots have greater surface roughness than the disturbed plots.*

organisms is readily taken up by surrounding vascular plants, fungi, and bacteria (Mayland and MacIntosh 1966; Mayland et al. 1966; Stewart 1967; Jones and Stewart 1969). Vascular plants growing in biologically crusted soils show higher tissue concentrations of nitrogen than plants grown in uncrusted soils (Harper and Pendleton 1993; Belnap 1994, 1995; Belnap and Harper 1995). As with carbon, crusts contribute nitrogen to soils both under plants and in plant interspaces, thereby counteracting the tendency of these nutrients to concentrate around perennial plants.

3.4 Albedo

Soil albedo is a measure of the energy reflected off the soil surface. Dark surfaces absorb more energy, are warmer than light surfaces, and thus have lower albedo. Because soils with well-developed biological crusts are dark, they can be up to 23°F warmer than adjacent crusted surfaces (Fig. 3.1; Belnap 1995; Belnap, unpublished data). Disturbance of biological crusts increases albedo and therefore decreases soil temperatures. This affects many ecosystem processes. Metabolic processes, for example, including photosynthesis and nitrogen fixation, decrease at lower temperatures (see Sections 3.2 and 3.3; Nash 1996). Lower soil temperatures decrease microbial activity, plant nutrient uptake rates, and soil water evaporation rates; delay seed germination time; and decrease seedling growth rates. Timing of these events is often critical in deserts, and modifications can reduce species fitness and seedling establishment, which in turn may eventually affect plant community structure (Bush and Van Auken 1991). Changes in albedo can also affect animal populations. For instance, foraging times are often partitioned among ants, arthropods, and small mammals on the basis of soil surface temperature (Doyen and Tschinkel 1974; Wallwork 1982; Crawford

1991). In addition, many small desert animals are weak burrowers, and soil surface microclimates are of great importance to their survival (Larmuth 1978). Consequently, altering surface temperatures can affect desert ecosystems at numerous levels.

3.5 Effects on Vascular Plants

3.5.1 Seed Germination

Biological crusts can affect vascular plant germination. While small cracks and crannies on the soil surface are generally sufficient for small-seeded plants to lodge and germinate, most large-seeded plants need soil or plant litter cover to germinate. In deserts where plant litter is often limited in interspaces, large native seeds generally have self-burial mechanisms (such as hygroscopic awns) or are cached by rodents. Many exotic species, however, lack self-burial mechanisms. Because biological crusts stabilize soils, germination of such seeds can be inhibited in sites with well-developed crusts and low plant litter, as was recently demonstrated for the annual exotic grass, cheatgrass (*Bromus tectorum*), in both the field and laboratory (Larsen 1995; Kaltenecker et al. 1999a; Belnap, unpublished data). Though crusts can reduce germination of some seeds, seedling germination *per se* has not been shown to limit species density in desert plant communities. Rather, studies worldwide show vascular plant cover and structure are most often controlled by water and/or nutrient availability rather than other site factors (Mabbutt and Fanning 1987; Tongway and Ludwig 1990; Dunkerley and Brown 1995).

3.5.2 Plant Establishment and Cover

Biological soil crusts have not been shown to present a barrier to seedling root penetration once seeds germinate (Belnap, unpublished data; Pendleton and Meyer, unpublished data). This is in contrast to physical crusts, which often inhibit root penetration. Areas



Figure 3.2 Sandberg bluegrass (*Poa secunda*) growing in well-developed biological soil crusts in the northern Great Basin.

that have been lightly trampled (to keep crusts from developing) over a 5-year period that included both wet and dry years show no additional plant establishment (Belnap, unpublished data; Fig. 3.1). Many authors have shown that seedling establishment of both forbs and grasses is either not affected or is increased by the presence of biological soil crusts, on both coarse- and fine-textured soils (Fig. 3.2; St. Clair et al. 1984; Harper and St. Clair 1985; Eckert et al. 1986; Harper and Marble 1988; Lesica and Shelley 1992; Belnap 1993).

Numerous authors have reported that biological crusts either do not compete with vascular plants (Kleiner and Harper 1972, 1977a, b; Anderson et al. 1982b; Jeffries and Klopatek 1987; Beymer and Klopatek 1992) or that vascular plant cover is enhanced by the presence of a biological crust (Dadlich et al. 1969; Graetz and Tongway 1986; Rosentreter 1986; Mucher et al. 1988; Carleton 1990; Ladyman and Muldavin 1994; Ladyman et al. 1994). This suggests that the presence of plants can aid the survival of crustal components, perhaps because of microclimate conditions associated with clumped perennial vegetation (such as decreased soil surface temperatures, increased surface moisture due to shading, and decreased wind speed on the soil surface). A few authors have speculated that there is a negative relationship between cover of biological crusts and vascular plants (Savory 1988 reviewed in West 1990). However, this view is not supported by the numerous studies that have directly addressed this issue. Rather, it appears more likely that biological crusts simply cover soils unoccupied by vascular plants.

3.5.3 Nutrient Levels in Vascular Plants

Plants growing in biologically-crustated soil often show higher concentrations and/or greater total accumulation of various essential nutrients than do plants growing in adjacent, uncrusted soils (Belnap and Harper 1995; Harper and Belnap in press). In one study, leaf tissue nitrogen was 9% higher in the perennial shrub *Coleogyne*, 31% higher in the perennial forb *Streptanthella*, and 13% higher in the annual grass *Festuca* (*Vulpia*), for plants growing in biologically-crustated soil compared to plants in adjacent uncrusted soil. Dry weight of *Festuca* plants in the crusted soil was twice that of plants in the uncrusted soil (Belnap 1995; Belnap and Harper 1995). Nitrogen concentrations in leaf tissue of the biennial *Mentzelia multiflora* was higher in plants growing in a biologically-crustated area relative to plants from an adjacent sand dune that lacked a crust. In greenhouse experiments, nitrogen levels in *Sorghum halepense* were higher when the plant was in pots with cyanobacteria than when in pots without cyanobacteria. Dry weight of plants in pots with cyanobacteria were up to four times greater than in pots without cyanobacteria (Harper

and Pendleton 1993). Other authors have obtained similar results with other species (Shields and Durrell 1964; Brotherson and Rushforth 1983; Pendleton and Warren 1995).

Several mechanisms may explain this enhanced effect on vascular plant growth and nutrient status. Material blowing across biological soil crusts can become trapped, either accumulating within low pockets in the microtopography or sticking by exudate to cyanobacterial sheaths. These sheaths are phototropic, and if not buried too deeply, will push through loose soil and organic matter, further trapping or entangling soil in the process (Fryberger et al. 1988; Campbell et al. 1989; Gillette and Dobrowolski 1993). Danin et al. (1989) proposed a positive feedback loop in which crusts trapping fine particles create nutrient-rich microsites, increasing germination and growth of vascular plants, which in turn reduces erosion potential and increases accumulation of washed or wind-blown soil.

In addition, cyanobacterial sheath material is often coated with negatively charged clay particles. These clay particles are more nutrient rich than sand (Black 1968), as they bind positively charged macronutrients and prevent them from leaching through the soil profile (Belnap and Gardner 1993). Lange (1974) demonstrated that compounds in the gelatinous sheath material of several cyanobacteria taxa were able to chelate iron, copper, molybdenum, zinc, cobalt, and manganese. Four of the five genera shown to possess this ability (*Anabaena*, *Anacystis*, *Lyngbya*, and *Nostoc*) are commonly represented in biological crusts of western North American deserts (Shields and Durrell 1964). It is also possible that the nutrient differences result from thermal effects, as crusted soils are darker and warmer than uncrusted soils; nutrient uptake by vascular plants would occur at a higher rate.

Herbivores and other consumers may benefit directly from the enhanced nutrient status of plants grown in healthy, biologically-crusted soils (Belnap and Harper 1995). Indirect effects include positive correlations between soil mycorrhizae and microarthropod populations with the presence of well-developed biological soil crusts (Harper and Pendleton 1993; Belnap, unpublished data).

3.6 Water Relations

The effect of biological soil crusts on soil-water relations is highly site dependent. Level of crustal development (e.g., cover and relative composition of cyanobacteria, lichen, moss), climatic regimes, the amount of surface roughness, time since destructive disturbance, soil texture, and soil structure can all heavily influence hydrologic cycles at a given site. Soil texture is especially important and can

override any effect of biological soil crusts. For instance, soils high in shrink-swell clays have relatively low infiltration rates, regardless of biological crust presence or absence.

Research conducted under a variety of soil and climate conditions around the world shows variable and interactive effects of biological crusts and soil properties. Biological crusts influence soil hydrology because they alter soil surfaces. Aggregate stability, soil structure, organic matter, and rough microtopography are all attributes associated with superior hydrologic properties, and biological soil crusts enhance these attributes in soil (Booth 1941; Fletcher and Martin 1948; Shields and Durrell 1964) on both micro- and macro-scales (Belnap and Gardner 1993; Belnap 1994).

Infiltration rates are controlled by the interaction of water-residence time on a soil surface and the permeability of that surface.

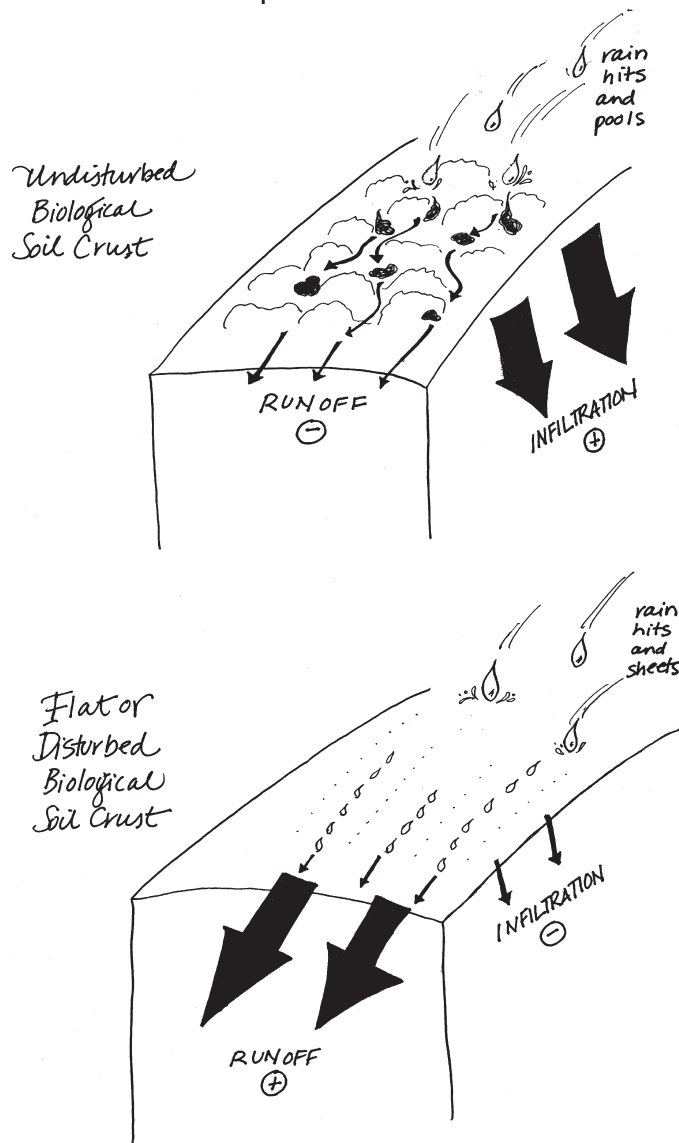


Figure 3.3 Soil-water relationships with biological soil crusts. In the cool deserts (Colorado Plateau, Great Basin), roughened soil surfaces created by biological crusts act to impede overland water flow, resulting in increased infiltration. When biological soil crusts are removed, or with flat crusts in the hot deserts (Sonoran, Mojave, Chihuahuan), water runs over the soil surface unimpeded and infiltration is reduced.

Biological crusts can produce a rough surface microtopography (less than 100 mm vertically) that acts as detention structures for water (Danin and Barbour 1982). This is especially pronounced in cool deserts (e.g., the Colorado Plateau), where frost-heaving is common and crusts are highly pedicelled. In these regions, biological crusts generally increase water infiltration (Fig. 3.3; Loope and Gifford 1972). In warm deserts, where frost-heaving is not present and biological soil crusts are flat, infiltration rates depend more on soil type and climatic regimes.

While greater surface roughness can increase water pooling and residence time, the presence of mucilaginous cyanobacteria in soil crusts can also decrease soil permeability. These cyanobacterial components of biological soil crusts rapidly swell up to 13 times their dry volume (Shields and Durrell 1964; Campbell 1977), potentially closing flow pathways through the soil surface. Scanning electron microscopy shows sufficient openings in sandy loam soils for water flow (Belnap and Gardner 1993), but concentration of silt and clay particles in the crust, in combination with swelling, may restrict infiltration even in sandy soils when they are wet (Verrecchia et al. 1995). Some authors speculate that the hydrophobic nature of some crustal components contributes to soil surface sealing (Bond 1964; Dulieu et al. 1977; Walker 1979; Rutin 1983; Jungerius and van de Meulen 1988); however, others have shown crustal organisms at some sites are highly hydrophilic (Kidron et al. 1999).

Overall, infiltration rates appear to be increased in regions where crusts are pinnacled and decreased in regions where crusts are flat. This has been reported for sandy soils in Arizona (Brotherson and Rushforth 1983), Australia (Bond 1964; Rogers 1977; Stanley 1983; Graetz and Tongway 1986; Eldridge 1993a, b), and Israel (Yair 1990). In New South Wales, Australia, infiltration rates increased on a transect through a sandy-loam soil as grazing decreased and biological soil crust cover increased. However, compared with adjacent ungrazed soils with a continuous cover of lichens and mosses, the lightly grazed areas showed greater infiltration (Eldridge 1993b). Infiltration studies conducted on sandy soils in Oklahoma and Kansas (Booth 1941) and silt-loams and clayey silt loams in Arizona (Faust 1970, 1971) failed to find any influence of biological soil crusts on infiltration rates.

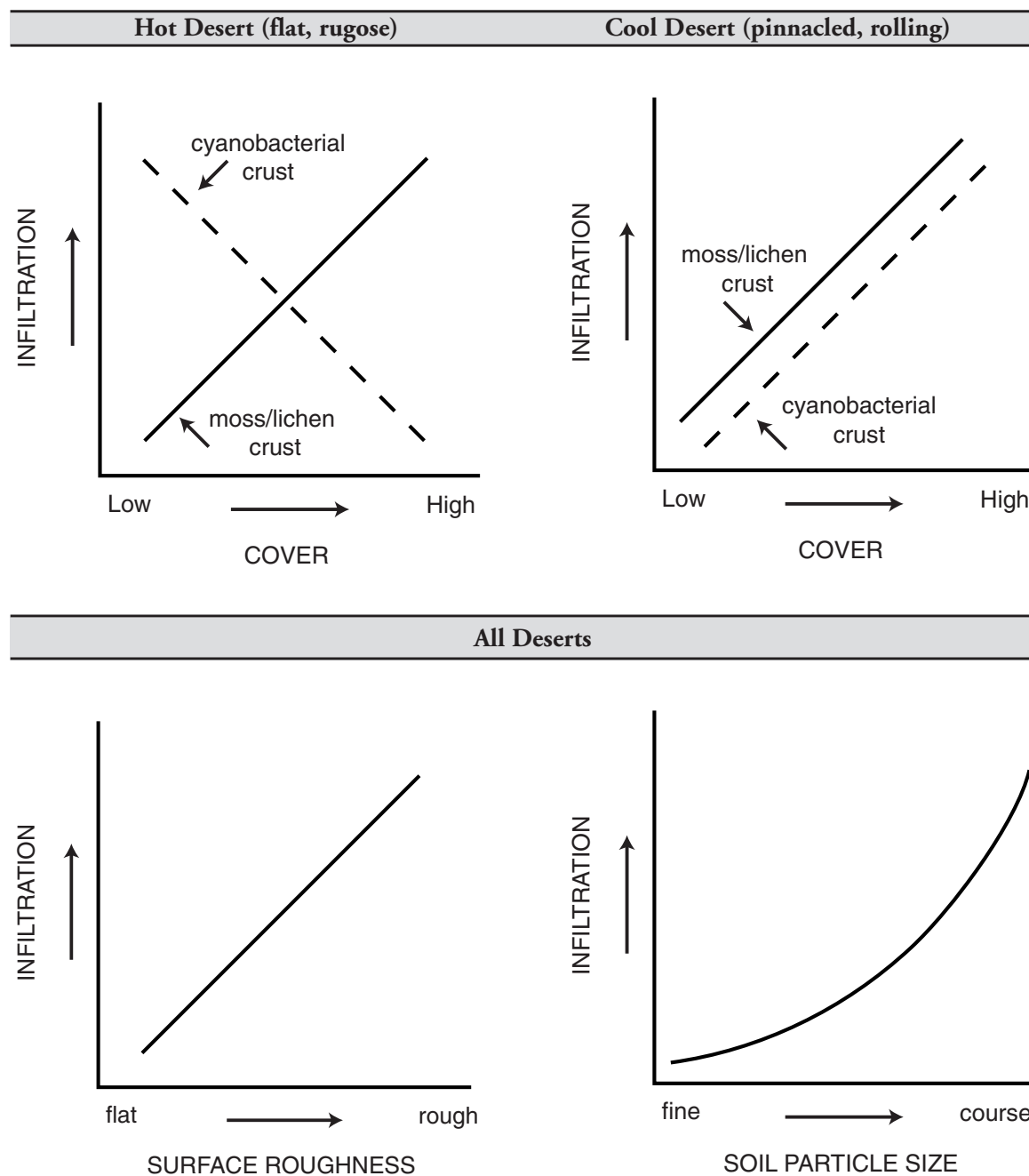
The influence of biological soil crusts on effective hydraulic conductivity (the rate at which water moves through the soil profile under field conditions) is also variable. Lichen-dominated crusts in Utah showed decreased hydraulic conductivity (Loope and Gifford 1972). Lichen and algal crusts in Australia were associated with high conductivity (Greene et al. 1990). Three-year-old algal crusts in Utah and non-disturbed crusts in Nevada showed no discernible influence on conductivity (Williams 1993; Dobrowolski 1994).

Biological soil crusts have varied effects on soil moisture at any given time. However, research results have been variable and again appear to depend on soil type and crust composition. The crust's ability to seal the soil surface and reduce evaporation because of its associated high clay and silt concentrations has been repeatedly proposed (Danin 1978; Brotherson and Rushforth 1983; Williams et al. 1995a). While some studies show soil moisture is greater under well-developed crusts (Harper and Marble 1988; Meyer and Garcia-Moya 1989; Verrecchia et al. 1995; Belnap et al. 1996), other studies have found decreased soil moisture under crusted surfaces (Harper and Marble 1988).

Though overall infiltration of precipitation is critical for plant growth, the location of water entering the soil can also be critical in maintaining plant community structure. Recent work has shown that the pattern of water infiltration and runoff is important in maintaining vegetative community structure, especially in hyper-arid zones where rainfall is too low to support homogenous distribution of vegetation. Instead of being distributed across the landscape, plants are concentrated in bands that occur perpendicular to the water flow. These bands or vegetation clumps capture water, nutrients, and fine soil particles. The bigger the bands, the more effective they are in resource capture; however, their overall size is limited by rainfall and nutrients. Biological soil crusts often cover interband soils. When these interband areas are disrupted, water infiltration can increase between vegetated areas; thus, less water is available for the vegetation, often deep-rooted, woody perennials (Eldridge et al. 2000). This decrease in water availability may lead to changes in plant community structure by enabling establishment of shallow-rooted species in the interband areas or by die-off of the perennial shrubs. Over time, changes in hydrology and plant community structure result in modification of site potential and ecological function. A similar situation applies to exotic plant invasions and their effects on site function. In the Great Basin, invasive exotic annual grasses modify the native community's patchy structure to a more homogenous structure (Kaltenecker 1997). The resultant increases in plant and litter density in interspaces previously occupied by biological crusts affect moisture infiltration, which may further facilitate changes in community structure because less moisture becomes available for deeply-rooted perennial plants.

As can be seen above, the impact of biological soil crusts on hydrologic cycles can be highly variable and can result from a combination of site, soil, and crust factors (Fig. 3.4). However, lack of standardized data collection methods and descriptions of soil, biological crust, and climatic characteristics at study sites makes comparison of research results difficult. These shortcomings have

Figure 3.4 *Biological soil crust and soil characteristics that influence infiltration.*



undoubtedly contributed to much of the seemingly contradictory published information.

3.7 Soil Stabilization

Biological soil crusts are unambiguously effective in reducing wind and water erosion of soil surfaces (Belnap and Gillette 1997, 1998; McKenna-Neumann et al. 1996). Wind can be a major erosive force in deserts, as sparse vegetation leaves large patches of soil unprotected by plant litter or vegetative cover (Goudie 1978). Interspace soils are most often stabilized by rocks or biological soil crusts. Biological crusts play an important role both in preventing soil loss and facilitating soil accretion. The degree to which different types of crusts protect the soil surface from both wind and water erosion is hierarchical in the following manner: bare soil < cyanobacterial/algal crust < lichen crust < moss crust (Tchoupopnou 1989; Kinnell et al. 1990; Eldridge and Greene 1994; Belnap and Gillette 1998). Polysaccharides exuded by cyanobacteria and green algae, in combination with lichen and moss rhizines, entrap and bind soil particles together, increasing the size of soil aggregates (Fig. 3.5). As soil aggregates enlarge, they become heavier, have a greater surface area, and are more difficult for wind or water to move. Biological soil crusts keep otherwise loose sandy soils in place on steep slopes; they also stabilize pockets of very shallow soil (Bond and Harris 1964; Marathe 1972; Gayel and Shtina 1974; Danin and Yaalon 1980; Schulten 1985; Graetz and Tongway 1986; Campbell et al. 1989; Danin et al. 1989; Belnap and Gardner 1993). Rough microtopography creates a still-air boundary layer that protects the soil surface from wind erosion. Detention dams pool and slow overland water flow, giving sediment time to settle out, reducing sediment loss (Fig. 3.3; Brotherson and Rushforth 1983; Alexander and Calvo 1990).



Fig. 3.5 The sheath of *Microcoleus vaginatus* contains sticky polysaccharides that entrap soil particles and bind them together.